



Responses of Native and Introduced Plant Species to Sucrose Addition in Puget Lowland Prairies

Authors: Kirkpatrick, H. Elizabeth, and Lubetkin, Kaitlin C.

Source: Northwest Science, 85(2) : 255-268

Published By: Northwest Scientific Association

URL: <https://doi.org/10.3955/046.085.0214>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Responses of Native and Introduced Plant Species to Sucrose Addition in Puget Lowland Prairies

Abstract

Nitrogen enrichment has often been demonstrated to enhance the success of introduced plant species at the expense of native species. In the south Puget lowland prairies of Washington State, invasion by Scotch broom (*Cytisus scoparius*), a nitrogen-fixing legume, is associated with elevated soil nitrogen levels. After broom removal, the higher soil nitrogen levels may have facilitated the secondary invasion of the prairies by numerous non-native species, particularly rhizomatous pasture grasses that can interfere with native plant seedling establishment. Numerous studies have shown the potential for carbon addition to immobilize soil nitrogen and reduce the success of introduced species relative to native species. We compared the available soil nitrate, the cover of native and introduced species between sugar-addition (1000 g C m⁻²) and control plots on two Puget lowland prairies. Sugar treatment initially immobilized nitrate and reduced cover of introduced species compared to that on control plots, but these effects dissipated within two years. Moreover, after four years, cover of introduced species, especially that of *Agrostis capillaris* and *Hypochaeris radicata*, had rebounded to become higher in sugar-addition than in control plots. In contrast, native species showed no negative responses to sugar treatment, suggesting that where sugar or other carbon treatment is economically feasible, combining carbon with the establishment of a high density of native species might limit the potential for introduced species to rebound.

Introduction

Habitats worldwide are subjected to nitrogen enrichment from anthropogenic sources (Driscoll et al. 2003, Fenn et al. 2003) and from invasive nitrogen-fixing legumes, which are disproportionately represented among invaders of native grasslands (Daehler 1998, Randall et al. 1998). Such legumes can dramatically increase available soil nitrogen (Witkowski 1991, Stock et al. 1995, Vitousek et al. 1997), and thereby have residual effects after their removal from the habitat (Maron and Jefferies 1999). Nitrogen enrichment of habitats that are naturally nitrogen-limited poses a significant conservation concern (Vitousek and Howarth 1991, Bakker and Berendse 1999) because of the well-documented negative effects of enrichment on plant species diversity (Aerts and Berendse 1988, Foster and Gross 1998, Stevens et al. 2004) and invasion (Huenneke et al. 1990, Wedin and Tilman 1990, Maron and Jefferies 1999). The combination of nitrogen enrichment and invasive species is particularly challenging for management of grasslands where the presence of a large component of native species restricts the available options for invasive

control. Restoration efforts that focus on the symptom (removing introduced species) but fail to address the underlying cause, presumably a shift in competitive abilities due to soil enrichment, may meet with limited success. In contrast, management techniques that attempt to address the underlying cause might meet with more success (Marrs 1993). In particular, techniques that reduce the soil nitrogen available to the plant community might restore the competitive balance in favor of native species. We evaluated the potential for carbon addition to reduce availability of soil nitrogen and enhance the competitive success of native species in the Puget lowland prairies of western Washington.

The Puget lowland prairies are one of the most endangered ecosystems in the United States (Noss et al. 1995). These prairie ecosystems support several taxa of national or statewide concern, including the mazama pocket gopher (*Thomomys mazama*), western gray squirrel (*Sciurus griseus*), golden paintbrush (*Castilleja levisecta*), white-topped aster (*Sericocarpus rigidus*), as well as a number of sensitive butterfly species (Schultz et al. 2011). However, less than 3% of these grasslands remain intact (Crawford and Hall 1997), and non-native species threaten the remainder. Scotch broom (*Cytisus scoparius*), a nitrogen-fixing shrub, has been the main invader of these prairies. Scotch broom has invaded and degraded grasslands

¹Author to whom correspondence should be addressed. E-mail: kirkpatrick@pugetsound.edu

²Current address: Environmental Systems Graduate Group, University of California, Merced, California 95344

across the Pacific Northwest by forming monocultures (Parker 2000). Like other nitrogen-fixing legumes (Witkowski 1991, Stock et al. 1995, Vitousek et al. 1997), Scotch broom has sometimes been shown to increase soil nitrogen (Haubensak and Parker 2004), and nitrogen enrichment appears to facilitate invasion of other non-natives (Corbin and D'Antonio 2003, Shaben and Myers 2010) or a decline in native species (Shaben and Myers 2010). There is also evidence that broom may have chemical inhibitory effects on native species (Haubensak and Parker 2004). Although the broom has been effectively controlled in portions of the Puget prairies (using herbicides, mowing, mechanical pulling, and fire), the nitrogen added by broom, as well as anthropogenic sources, may have facilitated invasion by other non-native species, particularly non-native perennial grasses that thrive under the higher nitrogen conditions (Mahmoud and Grime 1976). Despite ongoing control efforts, broom continues to re-establish from the long-lived seed bank, and many small plants bear root nodules (H.E.K., personal observation). Presumably, therefore, broom continues to enrich the soil to some extent, and there is likely some additional regional atmospheric deposition of nitrogen (Jefferies and Maron 1997), which has been estimated for the Pacific Northwest region by Galloway et al. (2004) as more than $250 \text{ mg N m}^{-2} \text{ yr}^{-1}$. Inkpen and Embrey (1998) estimated that atmospheric deposition of nitrogen constitutes almost 25% of the annual nitrogen load overall in the Puget Sound basin. Our research was directed at abating the threat from invasive non-native species, which is identified in The Nature Conservancy's draft South Puget Sound Prairies Site Conservation Plan and in their ecoregional assessment as one of the most urgent and severe stresses on many plant species conservation targets (Floberg et al. 2004).

Species Interactions, Soil Nitrogen, and Carbon Addition

Ecological experimentation has demonstrated that soil nitrogen levels can strongly influence species interactions, with native species from grassland habitats often showing a competitive advantage over weedy and invasive species at low nitrogen levels (Tilman and Wedin 1991, Wedin and Tilman 1993, Morgan 1994, Reeve Morghan and Seastedt 1999). In contrast, even very low increases in soil nitrogen levels through fertilization often can reduce plant diversity (Clark and Tilman 2008) and favor weedy and invasive species (Tilman and Wedin 1991, Wedin and Tilman 1993, Maron and Connors 1996, Cassidy et al. 2004, Vinton and Goergen 2006), and generally favor grasses over

forbs (Zavaleta et al. 2003). For example, Berendse et al. (1992) found that fertilized areas of Netherlands hayfields were dominated by invasive tall oatgrass (*Arrhenatherum elatius*) whereas unfertilized areas were dominated by native red fescue (*Festuca rubra*).

Given the positive responses of invasive species to added nitrogen and the tolerance shown by native grassland species to low nitrogen, reducing the levels of nitrogen available to plants should enhance the ability of native species to compete in a given site. The addition of organic matter with a high carbon:nitrogen (C:N) ratio has been suggested as a way to accomplish such, "reverse fertilization" (Hunt et al. 1988) through the following mechanism. All organisms require both carbon and nitrogen in their tissues. Whereas plants are most often limited by available soil nitrogen (LeBauer and Treseder 2008), most soil fungi and bacteria use decomposing organic matter as their energy source and are most often limited by the amount of reduced carbon energy in the soil. Therefore, adding a carbon source should increase soil fungal and bacterial populations and cause them to sequester nitrogen from the soil, making less nitrogen available to plants (Wilson and Gerry 1995, Blumenthal et al. 2003, Perry et al. 2010).

Carbon has been added by previous researchers in a number of forms including straw, organic mulch, sawdust, and sucrose sugar. Of these amendments, sawdust and sugar tend to be most common, applied either separately or in combination (Bleier and Jackson 2007, Haubensak et al. 2007). Because sugar is soluble and easily digested by the soil microbial community, it presumably has a rapid but short-lived effect. Sawdust and other more complex carbon sources tend to have slower but longer-term effects (Szili-Kovács et al. 2007). Because of their contrasting effects, sugar and sawdust are often used in combination to provide both rapid and long-term pools of reduced carbon.

Quite a number of studies have examined the potential for carbon amendments to alter plant species interactions, and some of these have demonstrated the differential responses of grasses and forbs or natives and invasive species. Alpert and Maron (2000) found that added sawdust reduced non-native species biomass by 40% compared to control areas, and that most of this reduction was due to reduced growth of invasive grasses. Often both native and non-native species show negative responses, but the non-native species' responses are more extreme. For example, Bleier and Jackson (2007) found that carbon addition suppressed the growth of both *Andropogon gerardi*, a native grass, and *Bromus inermis*, an invasive grass, but it had a much

larger negative effect on *Bromus inermis*. Blumenthal et al. (2003) showed a negative linear response of total weed biomass to increasing rates of added carbon (0 to 3346 g C m⁻²). However, species within functional groups do not all respond similarly; Blumenthal et al. (2003) also reported that, although their carbon addition treatment reduced the biomass of six annual weeds, it increased the biomass of one annual weed and three perennial weeds, as well as six native prairie species. Overall, there seems to be a general effect: Haubensak et al. (2007) combined the results of 50 carbon addition studies in a meta-analysis and found a strong negative effect of carbon addition on non-native species and a weak positive effect on native species. Moreover, in a recent review of 50 studies using various methods (burning, grazing, biomass removal, topsoil removal, and carbon addition) to lower soil nitrogen availability to control plant invasion, Perry et al. (2010) concluded that carbon addition, along with enhancing the establishment of desirable species tolerant of low-nitrogen, was the most promising approach to date. While these results provide support for using carbon addition as a tool to manage invasive species, the responses of plant species will also depend on the local biotic and abiotic environment (Pennings et al. 2005).

We established a field experiment in early 2006 to assess the responses to carbon addition of native and introduced species from the Puget lowland prairie community. We chose to add carbon in the form of sugar (sucrose) for two reasons. First, the prairies in which we worked contain a relatively large component of native species, and incorporating any carbon amendment into the soil, as is typically done when establishing a novel planting of native species, would have caused excessive damage to these extant natives. Therefore, we needed a soluble carbon source that could leach into the soil. Second, seeds of many of the native forb species require contact with mineral soil for successful germination (Agee 1993, Drake and Ewing 1997, Dunn 1998). Adding a surface treatment of sawdust or other non-soluble carbon source would cover the mineral soil and prevent new recruitment of these native species. However, adding sugar can increase the osmotic potential of the soil (Davis and Wilson 1997, Eschen et al. 2006), perhaps to the point of causing negative responses in the less drought-tolerant summer dormant species. Our specific goals were to examine the impact of sugar addition on soil nitrate, on the cover of native and introduced species, both in total and for selected individual species, as compared with untreated controls, in the south Puget lowland prairies.

In particular, we set up our experiment to test whether sugar addition would:

- result in lower available soil nitrate in these prairies,
- reduce introduced species cover, and if so, whether introduced species would be affected more than native species,
- enhance native species cover, presumably through a reduction in competition from introduced species,
- affect re-establishment of Scotch broom, positively or negatively, or
- affect the native spring-blooming, summer-dormant species, which are likely to be less drought tolerant than the summer-blooming species.

Because sugar is presumed to be metabolized quickly, we anticipated that any of these responses would be apparent within the first year after sugar addition. Indeed, very few studies of sugar addition have reported responses beyond two years post-treatment, and none to our knowledge report whether the community has returned to its pre-manipulation state. However, we cannot assume that the sugar addition has no long term effects. Therefore, we followed the responses for four years post-treatment.

Study Area

Mima Mounds Natural Area Preserve (46° 53'19"N, 123° 03'01"W; Washington State Department of Natural Resources) and Scatter Creek Wildlife Area (46° 50'47"N, 123° 00'21"W; Washington State Department of Fish and Wildlife) are both protected areas, managed by their respective agencies to enhance native species, among other goals. The prairies of the Puget lowlands are underlain with glacial outwash from the Vashon glacier (Del Moral and Deardorff 1976, Kruckeberg 1991). Mima Mounds exhibits extensive areas of mound and swale landform whereas Scatter Creek has very few mounds. Since the soils are formed from coarse glacial outwash, the prairie soils are naturally low in nitrogen and droughty (Giles 1970, Ugolini and Schlichte 1973, Crawford and Hall 1997), but the presence of an impervious layer under the shallow swale soils causes these soils to be wetter in the winter and drier in the summer than the soils on the mounds.

In the past, essentially all of Scatter Creek and much of Mima Mounds were heavily invaded by non-native Scotch broom, a nitrogen-fixing legume shrub that has invaded most of the non-forested areas of western Washington. Intensive effort has resulted in the successful suppression of Scotch broom from most of these two prairies, but a persistent Scotch broom seed

bank remains, which requires constant maintenance to prevent re-establishment of seedlings. Scotch broom had been controlled for several years in most of the areas in Mima Mounds prairie on which we worked before we initiated our experiments. However, in two of the three areas in Scatter Creek, substantial broom stands were mowed just prior to the initiation of our experiments. During the first two years of our experiments, we removed all broom seedlings and broom regrowth that appeared in the experimental plots. However, in 2009, broom regrowth was not removed and seedlings and regrowth were used to assess any effect of the treatments on Scotch broom recurrence.

Methods

In March 2006, as part of a larger experiment, we applied a total of 1000 g C m⁻² as sucrose (42% carbon) in three increments, each two weeks apart, to four 1-m² plots for comparison with four control plots on each of three areas in each of the two prairies (a total of 24 sugar-addition plots and 24 control plots). Sugar was applied in a randomized block experimental design, in which the treatments were replicated equally within the three blocks on each prairie and across the two prairies. We chose 1000 g C m⁻², a middle-to-high range among those applied in previous studies, as a compromise between cost and likelihood of showing an effect.

Soil nitrate was measured in soil samples (0-10 cm depth) from each plot collected in March 2006 (pre-treatment), April 2007, June 2009, and April 2010. Soils were stored at -20 °C until they were analyzed for nitrate, which was done colorimetrically in 2006 and 2007 and using a nitrate-selective electrode in 2009 and 2010. Each year, a subset of the soil nitrate values were verified through professional testing (USAg Analytical Services, Pasco, WA). The differences in soil collection dates were unavoidable; because soil nitrate levels change during the season, these differences in sampling dates may have caused some of the final differences among years. Therefore, although we present these data, caution should be exercised in the interpretation of differences among years.

Cover of each vascular plant species present, as well as total cover of moss and lichen, was estimated in each plot in late May-early June of 2006, 2007, 2009, and 2010, when most species could be reliably identified. In addition, in April of 2007 and 2009, we estimated the cover of the early summer-dormant species that senesce before the main census. Moss and lichen cover did not differ in any consistent way between treatments or from year to year and we did not consider it further.

Statistical Analysis

Across the four years and between the sugar treatments and prairies, we compared soil nitrate levels, total cover of native and introduced species, change in percent cover of native and introduced species, and cover of seven individual species based on their high abundances in the prairies, four native (Roemer's fescue [*Festuca idahoensis* ssp. *roemerii*], camas [*Camassia quamash*, 2007 and 2009 only], long-stolon sedge [*Carex inops*] and round-leaved bellflower [*Campanula rotundifolia*] and three introduced (colonial bentgrass [*Agrostis capillaris*], tall oatgrass [*Arrhenatherum elatius*], and hairy cat's ear [*Hypochaeris radicata*]). In addition, we compared cover of Scotch broom seedlings between control and sugar-addition plots for 2009 and 2010. For comparisons between treatments, we used t-tests when normality and homogeneity of variance assumptions were met, either directly or after natural log transformation (adding one before transformation when the data included zeros); where transformations were unsuccessful in attaining homogeneous variances, we used Mann-Whitney U tests for independent comparisons. To test for changes in cover across the four years of our study, we compared cover between years using paired t-tests, either with the pooled treatments (if they did not differ) or separately for individual treatments where treatments differed, applying Bonferroni corrections to the *P*-values for the multiple tests (e.g., for six yearly comparisons, *t*-values are reported without correction, but *P*-values were multiplied by six). Because Bonferroni corrections are highly conservative tests (Moran 2003), in these cases we refer to any result as significant if *P* < 0.10. Although most comparisons between control and sugar-addition plots did not differ between prairies, cover of individual species differed between prairies in several analyses. Therefore, we split all analyses by prairie for consistency, and sample sizes were 12 plots in each treatment for every analysis. Finally, to explore possible reasons for the increase in total cover in control plots as well as in sugar-addition plots over the four years of the experiment, we examined the relationship between native and introduced species' cover and total precipitation during the previous summer (June-September) from weather data collected at the Olympia, WA, airport (located approximately 17 km from each of our prairie sites; NOAA, Olympia airport station, <http://www.ncdc.noaa.gov/oa/climate/station-locator.html>) using ANCOVA, with sugar treatments and prairies as categorical variables. When interaction terms were not significant, they were deleted and the model was recalculated. All statistical analyses were

carried out using SPSS 13.0 for Windows. Nomenclature and native status follows the “USDA Plants” website (<http://plants.usda.gov/>).

Results

Soil Nitrate

Soil nitrate did not differ significantly between control and sugar-addition plots before the sugar treatments were applied (Mima Mounds: $t = 0.843$, $P = 0.408$; Scatter Creek: $t = 0.408$, $P = 0.687$; Figure 1, 2006). Over the first year, average nitrate concentration decreased in both treatments, but decreased twice as much in sugar-addition plots as in control plots, such that in 2007, the sugar-addition plots contained only 61.4% (Mima Mounds) and 50.3% (Scatter Creek) as much available nitrate as control plots (Mima Mounds: $t = 2.686$, $P = 0.013$; Scatter Creek: $t = 0.715$, $P = 0.482$). In 2009 and 2010, nitrate levels in the sugar-addition plots did not differ from those in the control plots (2009-Mima Mounds: $t = 0.208$, $P = 0.837$; Scatter Creek: $t = 0.155$, $P = 0.879$; 2010-Mima Mounds: $t = 0.726$, $P = 0.426$; Scatter Creek: $t = 1.479$, $P = 0.153$). Over the four

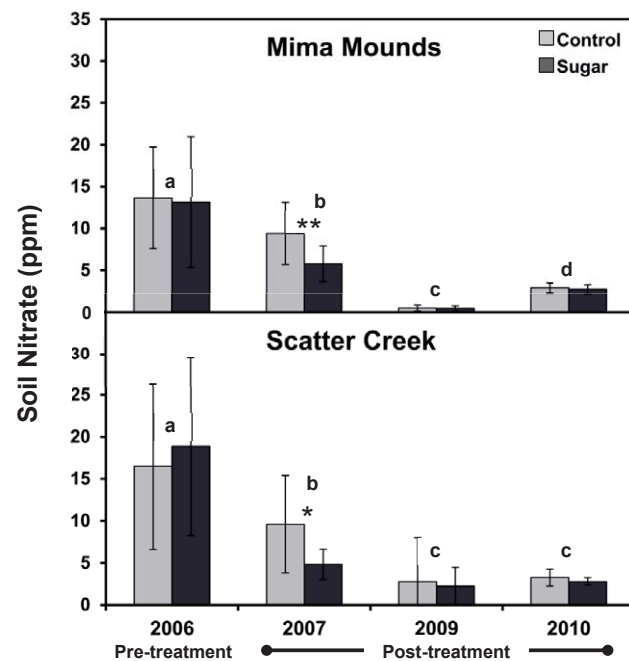


Figure 1. Mean soil nitrate levels (± 1 SD) in control and sugar-addition plots over four years in two south Puget lowland prairies ($N = 12$). Sugar (1000 g C m^{-2}) was added only in 2006, after the initial nitrate measurements, and all other nitrate measurements were post-treatment. Asterisks indicate significant differences between sugar treatments ($*P < 0.05$, $**P < 0.01$). Letters above the bars indicate differences among years; bars that share a letter are not different at $\alpha = 0.05$.

years of the study, nitrate levels within prairies and sugar treatment fell sharply, even in the control plots, such that every annual comparison indicated significant declines except 2009 to 2010 in Mima control plots, in which nitrate increased, and except 2006 to 2007 in Mima Mounds control plots and in 2009 to 2010 Scatter Creek control and sugar-addition plots which indicated no significant change (paired t-tests with Bonferroni corrections; for all significant comparisons $t > 3.421$ and $P < 0.010$). Only in 2009 did the two prairies differ in soil nitrate (Mann-Whitney U tests; $Z = 3.413$, $P < 0.001$), with Mima Mounds averaging only 20% as much nitrate as Scatter Creek. In all other years, the prairies did not differ in their soil nitrate levels (Mann-Whitney U tests; all $Z < 1.340$, all $P > 0.180$).

Total Native and Introduced Species Cover

In May 2006, only two months after the sugar additions, cover of introduced species was 42.4% lower (Mima Mounds) and 48.0% lower (Scatter Creek) in sugar-addition plots than in control plots (Mima Mounds: $t = 3.864$, $P < 0.001$; Scatter Creek: $t = 2.588$, $P = 0.017$; Figure 2, 2006). In contrast, native species showed no difference between sugar-addition and control plots (Mima Mounds: all $t = 0.144$, all $P = 0.887$; Scatter Creek: all $t = 0.419$, all $P = 0.680$). By May 2007, however, the effects of sugar addition on introduced species had dissipated, and although the absolute means of both native and introduced species were somewhat lower in the sugar-addition plots, neither plant group showed any significant responses to sugar treatments (Mima Mounds natives: $t = 0.944$, $P = 0.355$; introduced species: $t = 1.145$, $P = 0.264$; Scatter Creek-natives: $t = 0.855$, $P = 0.402$; introduced species: $t = 1.507$, $P = 0.146$). By 2009, cover of introduced species was 32.0% higher (Mima Mounds) and 51.3% higher (although not significantly, Scatter Creek) in sugar-addition plots than in control plots (Mima Mounds: $t = 2.077$, $P = 0.05$; Scatter Creek: $t = 1.670$, $P = 0.109$), whereas natives showed no differences (Mima Mounds: $t = 0.450$, $P = 0.657$; Scatter Creek: $t = 0.207$, $P = 0.838$). In 2010, although introduced species were still somewhat more abundant in sugar-addition plots than in control plots in Scatter Creek, this difference was no longer significant (In transformed data, $t = 0.696$, $P = 0.174$).

Both the difference in response to the sugar treatment between native and introduced species and a marked increase in total cover by both plant groups (see Responses to Precipitation, below) over the four year period are sharpened by comparing changes in cover between the two plant groups between 2006 and 2010 (Figure 3).

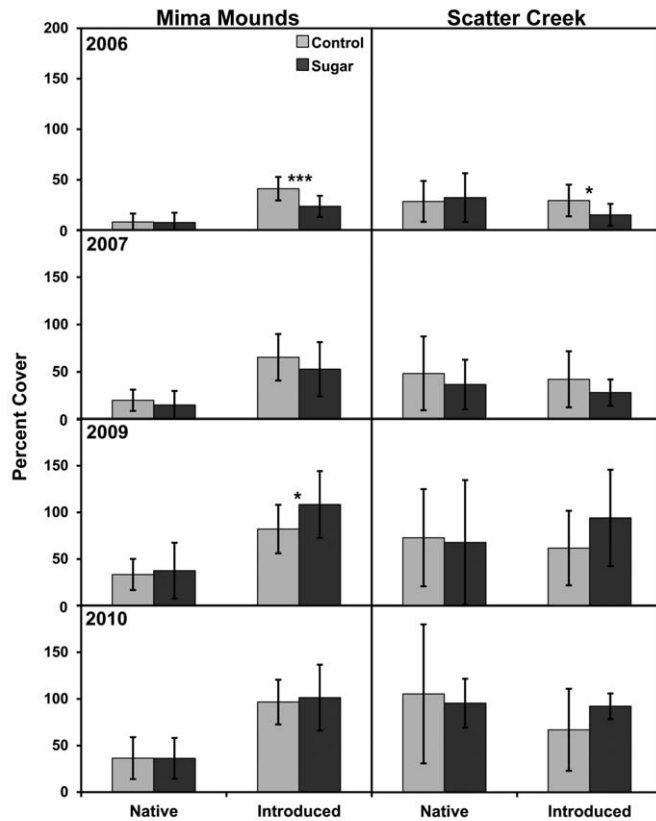


Figure 2. Mean cover (± 1 SD) of native and introduced species in control and sugar-addition plots over four years in each prairie ($N = 12$). Sugar (1000 g C m^{-2}) was added only in 2006, and all cover measurements were post-treatment. Asterisks indicate significant differences between sugar treatments (** $P < 0.05$, *** $P < 0.001$).

Native species showed similar increases in cover over the four years in both control and sugar-addition plots (Mima Mounds: control 28.1%, sugar-addition 28.4%; Scatter Creek: control 76.9%, sugar-addition 63.2%), which were not significantly different (ln transformed, Mima Mounds: $t = 0.096$, $P = 0.924$; Scatter Creek: $t = 0.953$, $P = 0.351$). In contrast, introduced species showed considerably larger increases in cover over the four years in sugar-addition than in control plots (Mima Mounds: control 55.3%, sugar-addition 77.1%; Scatter Creek: control 37.5%, sugar-addition 76.9%); these larger increases were significant in Scatter Creek (ln transformed, Mima Mounds: $t = 1.707$, $P = 0.102$; Scatter Creek: $t = 2.777$, $P = 0.011$). This difference in response to sugar addition between native and introduced species was marginally significant for both prairies (ANOVA Mima Mounds interaction $F_{1,44} = 2.962$, $P = 0.092$; Scatter Creek ln transformed interaction $F_{1,44} = 2.857$, $P = 0.098$, Table 1).

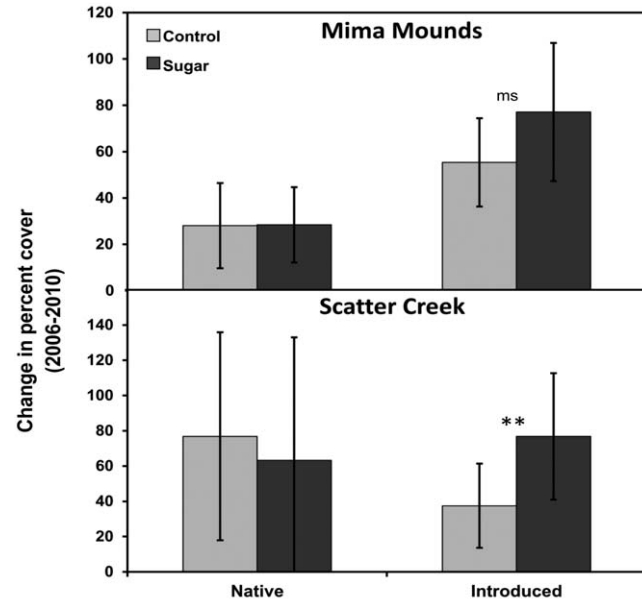


Figure 3. Mean change in cover (± 1 SD) of native and introduced species in control and sugar addition plots over four years in each prairie ($N = 12$; ms: $P < 0.01$).

TABLE 1. ANOVA tables comparing change in cover from 2006 to 2010 in Mima Mounds and Scatter Creek prairies between control and sugar addition treatments in native and introduced plant species.

Source	df	Mean Square	F	P
Mima Mounds				
Sugar Treatment	1	1465.78	3.161	0.082
Native Status	1	17310.90	37.335	<0.001
Treatment*Status	1	1373.34	2.962	0.092
Error	44	463.66		
Scatter Creek (ln transformed data)				
Sugar Treatment	1	0.01	0.022	0.883
Native Status	1	0.11	0.180	0.673
Treatment*Status	1	1.78	2.857	0.098
Error	44	0.62		

Responses of Individual Species

Introduced species – Cover of individual introduced species varied both between prairies and in response to sugar addition, but across prairies, treatments, and years, the three most abundant introduced species were hairy cat's ear (*Hypochaeris radicata*), colonial bentgrass (*Agrostis capillaris*), and tall oatgrass (*Arrhenatherum elatius*). Cover of hairy cat's ear was initially lower in sugar-addition plots than in control plots in 2006, but only significantly so for Mima Mounds because of the low initial cover in Scatter Creek (ln transformed data; Mima Mounds: 36% lower, $t = 3.695$, $P = 0.001$; Scatter Creek: 71.3% lower, $t = 0.634$, $P = 0.533$; Figure 4). It remained lower in 2007,

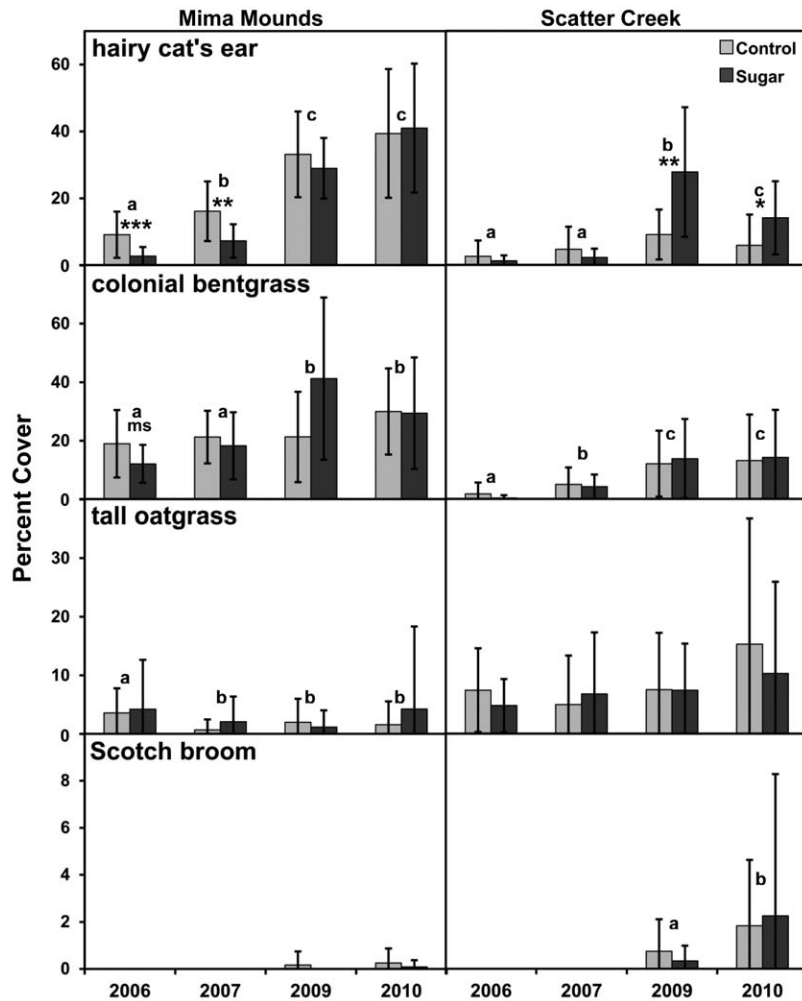


Figure 4. Mean cover (± 1 SD) of the four most abundant introduced species in control and sugar-addition plots in 2009 ($N = 12$). Asterisks indicate significant differences between sugar treatments (ms: $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Letters above the bars indicate differences among years; bars that share a letter are not different at $\alpha = 0.05$.

although still not significantly so in Scatter Creek (In transformed data; Mima Mounds: 54% lower, $t = 2.865$, $P = 0.009$; Scatter Creek: 46.1% lower, $t = 0.725$, $P = 0.477$). By 2009, there was no longer any difference in cover between control and sugar-addition plots in Mima Mounds, but cover had markedly increased in Scatter Creek such that cover of hairy cat's ear was significantly higher in sugar-addition than in control plots (In transformed data: Mima Mounds: 0.5% lower, $t = 0.701$, $P = 0.491$; Scatter Creek: 228.4% higher, $t = 3.225$, $P = 0.004$). The increased cover of hairy cat's ear in sugar-addition plots in Scatter Creek persisted in 2010 (In transformed data; Scatter Creek: 134.2% higher, $t = 2.253$, $P = 0.035$).

In contrast to hairy cat's ear, colonial bentgrass cover was only marginally significantly lower in sugar-

addition plots than control plots in 2006, and then only for Mima Mounds because of the low total cover in Scatter Creek (In transformed data; Mima Mounds, 36.0% lower, $t = 1.786$, $P = 0.088$; Scatter Creek, 71.3% lower, $t = 0.913$, $P = 0.374$). After 2006, colonial bentgrass did not differ significantly between control and sugar-addition in any year or prairie (In transformed data; all $t < 1.549$, $P > 0.136$). However, colonial bentgrass increased considerably from 2007 to 2009 in both prairies (paired t-tests with Bonferroni corrections; Mima Mounds: 57.9% increase; $t = 2.585$, $P = 0.10$; Scatter Creek: 172.4% increase; $t = 3.529$, $P = 0.011$). From 2009 to 2010, colonial bentgrass cover remained essentially stable (Figure 4).

Tall oatgrass cover did not differ between control and sugar-addition plots in either prairie in any year (all $t < 1.075$; all $P > 0.294$), and was essentially stable over the four years in Mima Mounds after a significant decrease between 2006 and 2007 in the control plots (80% decrease; $t = 2.747$, $P = 0.019$). In Scatter Creek, tall oatgrass cover showed marginally significant increases between 2007 and 2009 and again between 2009 and 2010 (paired t-tests, $t = 1.822$, $P = 0.096$; $t = 1.912$, $P = 0.082$, respectively, Figure 4).

Whereas we had removed Scotch broom seedlings in the first two years of the study to maintain the treatments, we stopped removals in 2009 and 2010 to test for effects of sugar additions on Scotch broom recurrence. By 2009, Scotch broom had recurred in about 17% of the plots (one of 12 control and none in sugar-addition plots in Mima Mounds; four of 12 control and three of 12 sugar-addition plots in Scatter Creek), and cover was low in plots where it occurred (1-2% cover). Between 2009 and 2010, broom had recurred in an additional two plots in Mima Mounds, and cover increased 244% in control 675% in sugar-addition plots in Scatter Creek, although these increases were not statistically significant because of the small sample sizes (Mann-Whitney U test, all $Z < 0.577$; all $P > 0.571$, Figure 4). In Scatter Creek in 2010, broom cover in occupied sugar-addition plots was 36% higher than in occupied control plots, but again this difference was not significant because of the low sample sizes (Mann-Whitney U test, $Z = 0.535$, $P = 0.629$).

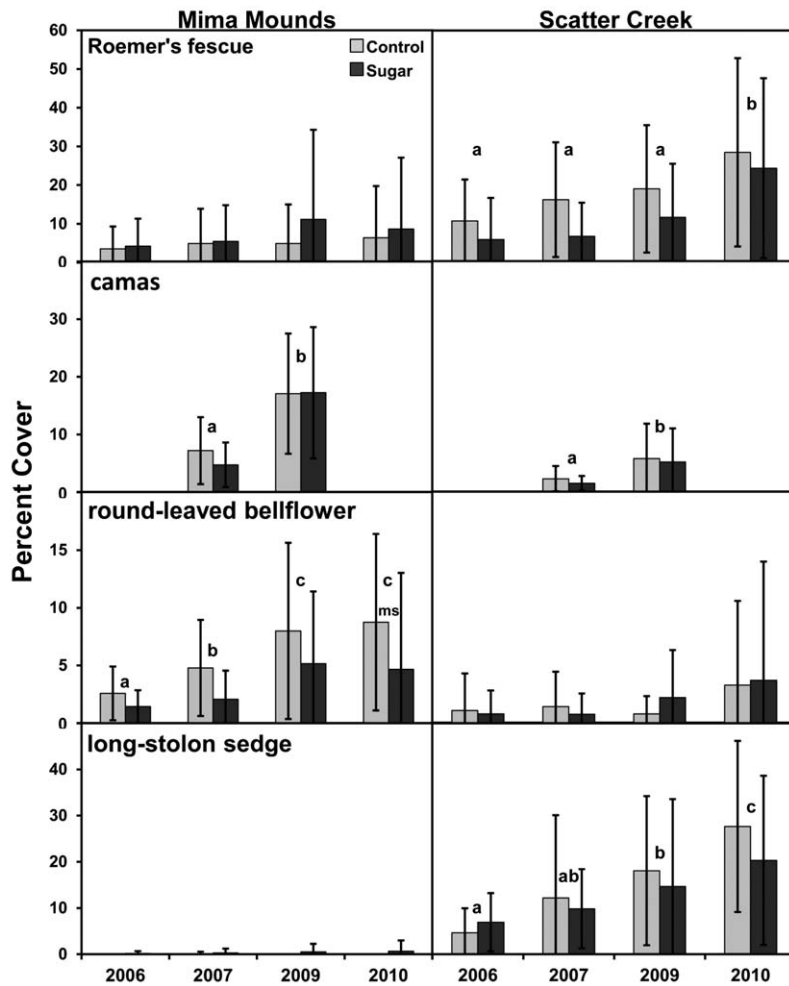


Figure 5. Mean cover (± 1 SD) of the four most abundant native species in control and sugar addition plots over four years ($N = 12$). There were no significant differences between sugar treatments (ms: $P < 0.10$). Letters above the bars indicate differences among years; bars that share a letter are not different at $\alpha = 0.05$.

Native species – Of the four most common native species in the prairie (Roemer's fescue, camas, round-leaved bellflower, and long-stolon sedge), none was significantly affected by sugar addition (Figure 5). Camas was of particular interest because it is one of the flagship prairie species, and it blooms early and senesces before the onset of the summer dry season. In 2007, camas cover was 34% lower on each prairie in the sugar-addition plots than in control plots, but these differences were not significant (Mima Mounds: $t = 1.220$, $P = 0.235$; Scatter Creek: $t = 1.058$, $P = 0.301$), and in 2009, the mean camas cover in control and sugar-addition plots was essentially identical (Mima Mounds: 17.1% vs. 17.2%, respectively; $t = 0.037$, $P = 0.971$; Scatter Creek: 5.8% vs. 5.1%, respectively; $t = 0.241$, $P = 0.812$). Similarly, although round-leaved bellflower cover was nominally lower in sugar addition

plots throughout the four years, this difference was marginally significant only on Mima Mounds in 2010 (ln transformed data; $t = 1.911$, $P = 0.069$; all other comparisons, $t < 1.667$, $P > 0.110$).

Across the four years of the study, however, cover of each of these native species (pooled over treatments) increased markedly in at least one of the prairies. Roemer's fescue cover remained stable at Mima Mounds but increased by 212% between 2006 and 2010 on Scatter Creek (paired t-tests with Bonferroni corrections, $t = 4.305$, $P = 0.001$). Cover of camas more than doubled on each prairie between 2007 and 2009, increasing by 187% on Mima Mounds and by 193% on Scatter Creek (paired t-tests, Mima Mounds: $t = 5.156$, $P < 0.001$; Scatter Creek: $t = 3.323$, $P = 0.003$). Round-leaved bellflower cover increased on both prairies between 2006 and 2010, but with the increases significant on only Mima Mounds (paired t-tests with Bonferroni corrections; Mima Mounds: 234% increase, $t = 3.353$, $P = 0.017$; Scatter Creek: 286% increase, $t = 1.862$, $P = 0.450$). Long-stolon sedge was almost absent on Mima Mounds, but it was abundant on Scatter Creek, and there it steadily increased over the four years such that by 2010, cover had increased 316% from 2006 (paired t-test with Bonferroni correction; $t = 5.614$, $P < 0.001$).

Cover Response to Precipitation

Analysis of weather records revealed a significant relationship between precipitation during the previous summer period (June–September) and plant cover measured in 2007, 2009 and 2010 (Table 2, Figure 6). Native species cover was higher in Scatter Creek than in Mima Mounds and this difference between the prairies increased only non-significantly with higher precipitation. In contrast, whereas introduced species cover showed no obvious relationship with prairie or sugar treatment under lower precipitation, it increased with higher precipitation significantly more in the sugar-addition plots than in the control plots ($F_{1,7} = 19.582$, $P = 0.003$).

Discussion

Sugar was effective in lowering soil nitrate levels significantly (by 44%, Figure 1), but only within the year following addition (2007). Based on literature reports of

TABLE 2. Cover responses of native and introduced species to sugar treatment and previous summer precipitation.

Source	df	Mean Square	F	P
Native Species				
Prairie	1	5067.630	35.111	<0.001
Sugar treatment	1	51.253	0.355	0.568
Precipitation*	1	2568.492	17.796	0.003
Error	8	144.331		
Introduced Species				
Prairie	1	1117.470	31.071	0.001
Sugar treatment	1	613.237	17.051	0.004
Precipitation*	1	4421.579	122.939	<0.001
Sugar*Precipitation	1	704.272	19.582	0.003
Error	7	35.966		

*Precipitation data were natural log transformed before analysis.

other studies using sugar (sucrose or dextrose; Reeve Morghan and Seastedt 1999, Paschke et al. 2000, Blumenthal et al. 2003, Suding et al. 2004, Paschke et al. 2005, Prober et al. 2005, Vinton and Goergen 2006, Bleier and Jackson 2007, Eschen et al. 2007, Blumenthal 2009), we expected a negative response of soil nitrate to sugar addition, but the duration of lower nitrate levels among previous studies varied, and most studies have not measured nitrate levels beyond a year after sugar addition. The effects we observed lasted a

year or more; unfortunately we were unable to collect data in 2008. By 2009, the effect had dissipated.

Cover of established native and introduced species initially supported our prediction that sugar treatment would give the native species a rapid, but short-lived, reduction in potential competition from non-native species. In May 2006 (Figure 2), only two months after sugar treatment, the cover of introduced species was significantly lower in sugar treated plots than in control plots, whereas native species showed no differences between the treatments. Although the same trend was apparent a year later, cover of neither introduced nor native species differed between control and sugar treated plots. In 2009, however, the pattern reversed, and introduced species cover was significantly higher in sugar treated plots than in control plots. A similar, though non-significant reversed trend persisted in 2010, the fourth year after sugar addition. This pattern of the introduced species gaining ground faster than the native species is most clear when comparing the change in cover from 2006 to 2010 between native and introduced species (Figure 3). This rebound of introduced species has not generally been noted in studies of sugar addition, perhaps because the studies do not continue to monitor the resident community long enough to see it. As is clear from the yearly cover means (Figure 2), total cover increased each year after sugar treatment.

Although the native species made up part of that increase, the introduced species increased more, both in the control plots and in the sugar-addition plots. Given that sugar addition doesn't actually remove nitrogen from the soil but presumably only induces the microbial community to sequester it, the stronger rebound of introduced species in sugar-addition plots might be caused by re-release of nitrogen once the microbial population has collapsed. Moreover, one

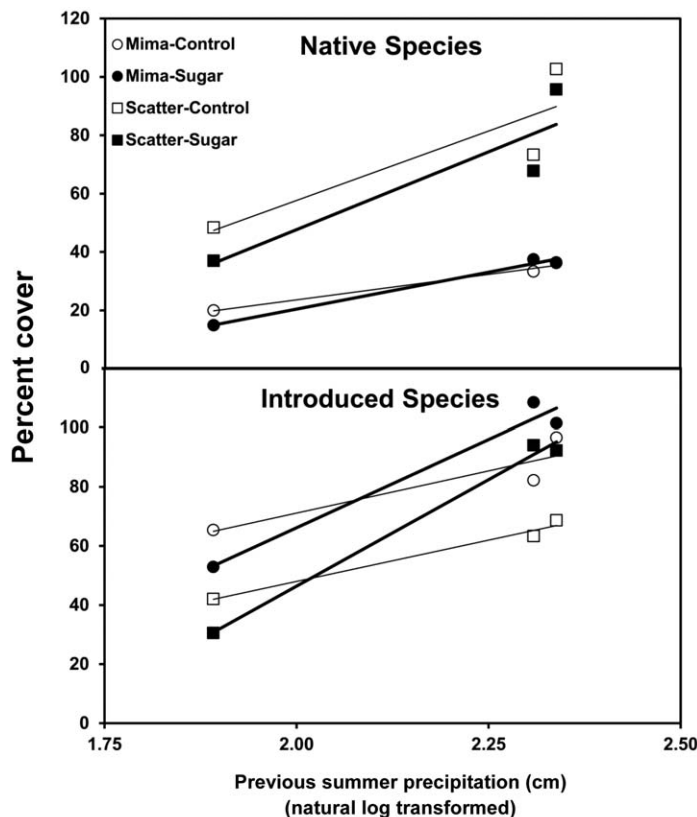


Figure 6. Association between cover of native and introduced species and total precipitation during the previous summer (June – September) in control and sugar-addition plots on each prairie. Each point represents the mean of 12 plots. Individual regressions: Native species, Mima Mounds, control treatment: $y = 34.828x - 46.006$, $R^2 = 0.986$, $P = 0.075$; sugar treatment: $y = 50.587x - 80.703$, $R^2 = 0.988$, $P = 0.068$; Scatter Creek, control treatment: $y = 94.993x - 132.24$, $R^2 = 0.762$, $P = 0.326$; sugar treatment: $y = 106.55x - 165.38$, $R^2 = 0.823$, $P = 0.277$; Introduced species, Mima Mounds, control treatment: $y = 57.182x - 43.258$, $R^2 = 0.834$, $P = 0.266$; sugar treatment: $y = 119.2x - 172.25$, $R^2 = 0.969$, $P = 0.113$; Scatter Creek, control treatment: $y = 55.884x - 63.773$, $R^2 = 0.983$, $P = 0.085$; sugar treatment: $y = 144.21x - 242.03$, $R^2 = 0.993$, $P = 0.053$. ANCOVA results are shown in Table 2.

mechanism by which species tolerate low resources is an inherently low relative growth rate (Chapin 1980, Grime 1988, Goldberg and Landa 1991), and the lack of response by the native prairie species, on a population level, is consistent with the hypothesis that they were unable to take advantage of the presumed lower competition provided by the initial lower biomass in the surrounding community and then also any released nitrogen. Although any re-release of nitrogen might have been evident in the soil nitrate data, it might also have been rapidly taken up by the plant community (Shaben and Myers 2010) preventing us from documenting it, especially since we sampled soil late in 2009.

The rebound of the introduced species is troubling for using sugar as a management tool; if sugar causes initial success but is detrimental in the longer term, it is clearly not a magic bullet, but a management tool to be considered for use in concert with other tools. The vast majority of sugar addition studies have followed plant cover for one to two years (or even less) because sugar is presumed to have only short-term effects. More studies need to follow the native and introduced plant cover responses for at least three years to assess the generality of the response we have documented. In addition, rebound might be prevented if sugar were added persistently (a “press” experiment), perhaps at lower concentrations, rather than only as a single application (a “pulse” experiment).

Among the most abundant introduced species, only hairy cat’s ear showed a significant individual negative response to sugar addition (Figure 3). Colonial bentgrass is the most abundant invasive grass in these prairies and tall oatgrass has been especially targeted for eradication by managers. Unfortunately, neither of these important invasive species was negatively affected by sugar addition; in fact, they both increased in the plots over the four years of the experiment. Colonial bentgrass, in particular, appears to be one of the introduced species that has rebounded after other resident species were suppressed by sugar addition. The overall significant reduction in introduced species in sugar-addition plots in 2006 must therefore be an accumulation of smaller non-significant responses by many introduced species (e.g., colonial bentgrass on both prairies, tall oatgrass on Scatter Creek). The trend toward lower Scotch broom cover in sugar-addition plots is suggestive, but because the difference is not significant, support for the suggestion that sugar has any effect on Scotch broom is weak at best.

Among native species, none showed a significant negative response to sugar addition. However, Ro-

emer’s fescue, the most abundant native species on both prairies, had consistently, although not significantly, lower abundances in the sugar-addition plots on Scatter Creek (although not on Mima Mounds [Figure 4]), suggesting that there may be some concern that fescue doesn’t tolerate sugar particularly well. However, previous work with this species (Ewing 2002) suggested that impoverishment of the soil—lowering nitrate availability—as we did in the sugar-addition plots, resulted in the best success of fescue in competition with introduced species. Therefore, it may not be the lower nitrate availability itself that is causing the nominally lower abundance of fescue, but other effects of the sugar (see below). In contrast to fescue, camas showed no negative effects of sugar addition, and in fact, showed a strong increase between 2007 and 2009. Camas differs from many of the early-blooming species in that it perenniates as a bulb, and therefore may be somewhat insulated from the effects of sugar. Round-leaved bellflower, another spring bloomer, had different responses to sugar on the two prairies: on Mima Mounds, cover in the sugar-addition plots was consistently, though not significantly, lower than in the control plots, whereas on Scatter Creek, cover of bellflower was nominally higher on sugar-addition plots than control plots by 2009. Finally, long-stolon sedge was slightly, although again not significantly, less abundant in the sugar-addition than in control plots on Scatter Creek. If these two species are representative of most of the early-blooming summer-dormant native species, this minimal negative response suggests that sugar would not particularly damage those species that provide the stunning floral show on the prairies in the spring. However, more tests of the effects of sugar on these summer-dormant species are necessary to generalize.

Adding natives via seeding or transplanting in combination with carbon addition to reduce soil nitrogen has been proposed (Funk and Vitousek 2007), and would presumably reduce the rebound of introduced species that we observed, but only if a sufficient density of native species were established. Also, the success of establishment is likely to be directly related to the cost. In most situations, transplantation would be the most successful way to increase the abundance of natives, but it is also the most expensive. Broadcast seeding is cheaper but often relatively ineffective because of low rates of establishment success due to complex germination or establishment requirements (Davies et al. 1999, Page and Bork 2005). Depending on the scope and goal of the restoration effort, the cost

of transplanting may indeed be prohibitive. Using a combination of transplants and seeding, or allowing a relatively small number of transplants to become seed sources themselves, might be a compromise solution for some restorations (Mulligan et al. 2002).

Although our study and many others (e.g., Paschke et al. 2000, Török et al. 2000, Cassidy et al. 2004, Prober et al. 2005, Eschen et al. 2007, and see also Perry et al. 2010) have demonstrated that sugar addition does immobilize nitrogen, which is often associated with a disproportional negative effect on introduced species, there is another possible mechanism to explain these observations. Sugar adds solute to the soil solution and therefore increases the osmotic potential of the soil. This increase in osmotic potential would make it more difficult for plant roots to draw water from the soil, inducing a physiological equivalent of drought, to which some species might be more tolerant than others. Most of the studies that have been successful in using sugar to enhance the relative success of native species have targeted relatively drought tolerant native species (e.g., Paschke et al. 2000, Cione et al. 2002, Blumenthal 2009), but certainly not all studies with drought-tolerant native species have successfully enhanced those natives (e.g., Reeve Morghan and Seastedt 1999). If desired native species are more drought tolerant than the introduced species, then the osmotic effects of sugar could be part of the cause of the differential response between native and introduced species, rather than solely nitrogen immobilization. Although these osmotic effects of sugar have largely gone unmentioned, at least one study has combined sugar addition with nitrogen addition to test for non-nitrogen effects of carbon addition (Blumenthal et al. 2003). They used a combination of sugar and sawdust as the carbon source, and their results suggest that nitrogen immobilization is responsible for the success of native species they observed. Only two other studies explicitly considered osmotic causes for some of their observations: Eschen et al. (2006) mentioned osmotic effects as a possible complication in their pot study, and Davis and Wilson (1997) suggested osmotic effects to explain the extensive mortality observed in their field sugar addition experiment. Of particular interest is that the desired native species in Davis and Wilson's experiment were wetland prairie species, which would likely be less drought-tolerant than the grassland species targeted by many studies. However, among those species that were killed by sugar in that experiment were woolly sunflower and colonial bentgrass, two species that were very tolerant of sugar additions in

our experiments. This outcome suggests that local adaptations are critical to species' responses.

The marked increase in cover over the four years of our study that we documented in both the control and sugar-addition plots was unexpected, and our data do not directly address its cause. However, analysis of local weather records resulted in some support for the hypothesis that these increases were weather-driven (Figure 6). The relationship between previous summer precipitation and cover the next year seems reasonable given the droughty soils and water limitation during the summer season on these prairies. More summer moisture would presumably lead to more stored carbohydrate, which would potentially result in larger plants or increased seedling establishment the following year. The rather striking pattern that introduced species increased much more than native species in response to the higher precipitation further supports the suggestion that the native species have inherently lower growth rates than the introduced species and cannot take advantage of available resources as quickly as can the introduced species.

The initial high levels of nitrate might be somewhat surprising since broom had been under management on these prairies for at least a decade prior to the initiation of our experiment, and leaching would presumably have reduced levels of nitrate over that time. Therefore, it seems that either there are sources of nitrogen deposition in the region other than Scotch broom (Inkpen and Embrey 1998) or that leaching doesn't remove nitrogen very rapidly. Given this observation, the noticeable decrease in nitrate levels in the control plots over the four years was also somewhat surprising. Yet we observed a rather steep decline in both the sugar-addition and the control plots from 2006 to 2009. One possible explanation is that we sampled nitrate at somewhat different times in these years; if nitrate levels decrease rapidly over the spring season, as found by Shaben and Myers (2010), then the low nitrate levels in June 2009 would potentially be an artifact of sampling time. However, both the 2008 and 2010 samples were taken in April, and the decline in nitrate is evident between these similar sampling dates. A second possible explanation is that the higher plant cover made possible by the previous summer's precipitation resulted in increased nitrate uptake by those plants, and less nitrate available the following year.

In summary, sugar addition was successful in immobilizing soil nitrate and, in the short term, in suppressing introduced species without suppressing native species. However, in the longer term, the overall

suppression of the resident community seems to have allowed the introduced species to rebound faster than the native species, and four years after sugar addition, introduced species have shown somewhat higher cover in the sugar-addition plots than in the control plots. Therefore, it may be advantageous to try a combination of transplantation (in small areas) and seeding (in larger areas) of low-nitrogen and drought tolerant native species with sugar additions to prevent the rebound of introduced species.

Literature Cited

- Aerts, R., and F. Berendse. 1988. The effect of increased nutrient availability on vegetation dynamics in wet heathlands. *Vegetatio* 76:63-69.
- Agee, J. K. 1993. *Fire Ecology of the Pacific Northwest Forests*. Island Press, Washington, D.C.
- Alpert, P., and J. L. Maron. 2000. Carbon addition as a countermeasure against biological invasion by plants. *Biological Invasions* 2:33-40.
- Bakker, J. P., and F. Berendse. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology and Evolution* 14:63-68.
- Berendse, F., W. Th. Elberse, and R. H. M. E. Geerts. 1992. Competition and nitrogen loss from plants in grassland ecosystems. *Ecology* 73:46-53.
- Bleier, J. S., and R. D. Jackson. 2007. Manipulating the quantity, quality, and manner of C addition to reduce soil inorganic N and increase C3:C4 grass biomass. *Restoration Ecology* 15:688-695.
- Blumenthal, D. M., N. R. Jordan, and M. P. Russelle. 2003. Soil carbon addition controls weeds and facilitates prairie restoration. *Ecological Applications* 13:605-615.
- Blumenthal, D. M. 2009. Carbon addition interacts with water availability to reduce invasive forb establishment in a semi-arid grassland. *Biological Invasions* 11:1281-1290.
- Cassidy, T. M., J. H. Fownes, and R. A. Harrington. 2004. Nitrogen limits an invasive perennial shrub in forest understory. *Biological Invasions* 6:113-121.
- Chapin, F. S., III. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11:233-260.
- Cione, N. K., P. E. Padgett, and E. B. Allen. 2002. Restoration of a native shrubland impacted by exotic grasses, frequent fire, and nitrogen deposition in southern California. *Restoration Ecology* 10:376-384.
- Clark, C. M., and D. Tilman. 2008. Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature* 451:712-715.
- Corbin, J. D., and C. M. D'Antonio. 2003. Too much of a good thing: Restoration of native biodiversity following soil nitrogen enrichment. In C. Piroosko (editor), *Proceedings of the California Invasive Plant Council Symposium*. Vol. 7:19-20.
- Crawford, R. C., and H. Hall. 1997. Changes in the south Puget prairie landscape. In P. V. Dunn and K. Ewing (editor), *Ecology and Conservation of the South Puget Sound Prairie Landscape*. The Nature Conservancy, Seattle, WA. Pp. 107-122.
- Daehler, C. C. 1998. The taxonomic distribution of invasive angiosperm plants: ecological insights and comparison to agricultural weeds. *Biological Conservation* 84:167-180.

Acknowledgements

The authors are indebted to Ashleigh Boyd, Megan Burgmuller, Lisa Fazzino, Sarah Hamman, Jason Heino, Emily Kahler, Maggie Klee, Blaine Marchant, Tanya Rogers, Megan Saunders, and Mary Wexman for help with field work, to the Washington State Departments of Natural Resources and Fish and Wildlife for access to the field sites, to Stacey Weiss, Peter Dunwiddie and two anonymous reviewers for improvements in the manuscript, and to The University of Puget Sound for funding.

- Davies, A., N. P. Dunnett, and T. Kendle. 1999. The importance of transplant size and gap width in the botanical enrichment of species poor grasslands in Britain. *Restoration Ecology* 7:271-280.
- Davis, K. J., and M. V. Wilson. 1997. Sugar, carbon treatment kills plants in soil impoverishment experiment (Oregon). *Restoration and Management Notes* 15:80-81.
- Del Moral, R., and D. C. Deardorff. 1976. Vegetation of the Mima Mounds, Washington State. *Ecology* 57:520-530.
- Drake, D., and K. Ewing. 1997. Germination Requirements of 32 Native Washington Prairie Species. In P. V. Dunn and K. Ewing (editors), *Ecology and Conservation of the South Puget Sound Prairie Landscape*. The Nature Conservancy of Washington, Seattle, WA. Pp. 181-187.
- Driscoll, C. T., D. Whitall, J. Aber, E. Boyer, M. Castro, C. Cronan, C. L. Goodale, P. Groffman, C. Hopkinson, K. Lambert, G. Lawrence, S. Ollinger. 2003. Nitrogen pollution in the northeastern United States: Sources, effects and management options. *BioScience* 53:357-374.
- Dunn, P. 1998. *Prairie Habitat Restoration and Maintenance on Fort Lewis and Within the South Puget Sound Prairie Landscape*. Final Report and Summary of Findings. The Nature Conservancy of Washington, Seattle, WA.
- Eschen, R., H. Müller-Schärer, and U. Schaffner. 2006. Soil carbon addition affects plant growth in a species-specific way. *Journal of Applied Ecology* 43:35-42.
- Eschen, R., S. R. Mortimer, C. S. Lawson, A. R. Edwards, A. J. Brook, J. M. Igual, K. Hedlund, and U. Schaffner. 2007. Carbon addition alters vegetation composition on ex-arable fields. *Journal of Applied Ecology* 44:95-104.
- Ewing, K. 2002. Effects of initial site treatments on early growth and three-year survival of Idaho fescue. *Restoration Ecology* 10:282-288.
- Fenn, M. E., J. S. Baron, E. B. Allen, H. M. Rueth, K. R. Nydick, L. Geiser, D. Bowman, J. O. Sickman, T. Meixner, D. W. Johnson, and P. Neitlich. 2003. Ecological effects of nitrogen deposition in the Western United States. *BioScience* 54:4040-420.
- Floberg, J., M. Goering, G. Wilhere, C. MacDonald, C. Chappell, C. Rumsey, Z. Ferdana, A. Holt, P. Skidmore, T. Horsman, E. Alverson, C. Tanner, M. Bryer, P. Iachetti, A. Harcombe, B. McDonald, T. Cook, M. Summers, and D. Rolph. 2004. *Willamette Valley-Puget Trough-Georgia Basin Ecoregional Assessment*. Prepared by The Nature Conservancy with The Nature Conservancy of Canada, Washington Department of Fish and Wildlife, Washington Department of Natural Resources, Oregon State Natural Heritage Information Center and the British Columbia Conservation Data Centre.

- Foster, B. L., and K. L. Gross. 1998. Species richness in a successional grassland: Effects of nitrogen enrichment and plant litter. *Ecology* 79:2593-2602.
- Funk, J. L., and P. M. Vitousek. 2007. Resource use efficiency in low resource systems. *Nature* 446:1079-1081.
- Galloway, J. N., F. J. Dentener, D. G. Capone, E. W. Boyer, R. W. Howarth, S. P. Seitzinger, G. P. Asner, C. C. Cleveland, P. A. Green, E. A. Holland, D. M. Karl, A. F. Michaels, J. H. Porter, A. R. Townsend, and C. J. Vörösmarty. 2004. Nitrogen cycles: past, present, and future. *Biogeochemistry* 70:153-226.
- Giles, L. J. 1970. The ecology of the mounds on the Mima Prairie, with special reference to Douglas Fir invasion. M.S. Thesis. University of Washington, Seattle.
- Grime, J. P. 1988. The C-S-R model of primary plant strategies: origins, implications, and tests. In L. D. Gottlieb and S. K. Jain (editors), *Plant Evolutionary Biology*. Chapman and Hall, London. Pp. 371-393.
- Goldberg, D. E., and K. Landa. 1991. Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *Journal of Ecology* 79:1013-1030.
- Haubensak, K. A., and I. M. Parker. 2004. Soil changes accompanying invasion of the exotic shrub *Cytisus scoparius* in glacial outwash prairies of western Washington (USA). *Plant Ecology* 175:71-79.
- Haubensak, K. A., K. G. Allcock, W. B. Mattingly, B. Swedo, L. M. Young, and H. L. Reynolds. 2007. Carbon addition to soils as a tool for restoration and research: a meta-analysis of patterns and mechanisms. Poster presentation at joint conference of the Ecological Society of America and Society for Ecological Restoration International, San Jose, CA.
- Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in California serpentine grassland. *Ecology* 71:478-491.
- Hunt, H. W., E. R. Ingham, D. C. Coleman, E. T. Elliott, and C. P. Reid. 1988. Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. *Ecology* 69:1009-1016.
- Inkpen, E. L., and S. S. Embrey. 1998. Nutrient transport in the major rivers and streams of the Puget Sound Basin, Washington. USGS Fact Sheet FS-009-98. Available online at <http://wa.water.usgs.gov/pubs/fs/fs.009-98/> (accessed 26 February 2011).
- Jefferies, R. L., and J. L. Maron. 1997. The embarrassment of riches: atmospheric deposition of nitrogen and community and ecosystem processes. *Trends in Ecology and Evolution* 12:74-78.
- Kruckeberg, A. R. 1991. *The Natural History of Puget Sound Country*. University of Washington Press, Seattle, WA.
- LeBauer, D. S., and K. K. Treseder. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* 89:371-379.
- Mahmoud, A., and J. P. Grime. 1976. An analysis of competitive ability in three perennial grasses. *New Phytologist* 77:431-435.
- Marrs, R. H. 1993. Soil fertility and nature conservation in Europe: Theoretical considerations and practical management solutions. *Advances in Ecological Research* 24:241-300.
- Maron, J. L., and P. G. Connors. 1996. A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia* 105:302-312.
- Maron, J. L., and R. L. Jefferies. 1999. Bush lupine mortality, altered resource availability, and alternative vegetation states. *Ecology* 80:443-454.
- Moran, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* 100:403-405.
- Morgan, J. P. 1994. Soil impoverishment: A little-known technique holds potential for establishing prairie. *Restoration and Management Notes* 12:55-56.
- Mulligan, M. K., L. K. Kirkman, and R. J. Mitchell. 2002. *Aristida beyrichiana* (Wiregrass) establishment and recruitment: implications for restoration. *Restoration Ecology* 10:68-76.
- Noss, R. F., E. T. LaRoe III, and J. M. Scott. 1995. *Endangered ecosystems of the U.S.: a preliminary assessment of loss and degradation*. Washington, D.C.: U.S. Dept. of the Interior, National Biological Service.
- Page, H. N., and E. W. Bork. 2005. Effect of planting season, bunchgrass species, and neighbor control on the success of transplants for grassland restoration. *Restoration Ecology* 13:651-658.
- Parker, I. M. 2000. Invasion dynamics of *Cytisus scoparius*: A matrix model approach. *Ecological Applications* 10:726-743.
- Paschke, M. W., T. McLendon, and E. F. Redente. 2000. Nitrogen availability and old-field succession in a shortgrass steppe. *Ecosystems* 3:144-158.
- Paschke, M. W., E. F. Redente, S. D. Warren, D. A. Klein, L. Smith, A. Klawitter, and T. McLendon. 2005. Integrated control and assessment of knapweed and cheatgrass on Department of Defense Installations. Technical Report number SERDP: CS1145. Strategic Environmental Research & Development Program, HydroGeoLogic, Inc. Herndon, VA.
- Pennings, S. C., C. M. Clark, E. E. Cleland, S. L. Collins, L. Gough, K. L. Gross, D. G. Milchunas and K. N. Suding. 2005. Do individual plant species show predictable responses to nitrogen addition across multiple experiments? *Oikos* 110:547-555.
- Perry, L. G., D. M. Blumenthal, T. A. Monaco, M. W. Paschke, and E. F. Redente. 2010. Immobilizing nitrogen to control plant invasion. *Oecologia* 163:13-24.
- Prober, S. M., K. R. Thiele, I. D. Lunt, and B. Koen. 2005. Restoring ecological function in temperate grassy woodlands: manipulating soil nutrients, exotic annuals and native perennial grasses through carbon supplements and spring burns. *Journal of Applied Ecology* 42:1073-1085.
- Randall, J. M., M. Rejmánek, and J. C. Hunter. 1998. Characteristics of the non-native flora of California. *Fremontia* 26:3-12.
- Reever Morghan, K. J., and T. R. Seastedt. 1999. Effects of soil nitrogen reduction on nonnative plants in restored grasslands. *Restoration Ecology* 7:51-55.
- Schultz, C. B., E. Henry, A. Carleton, T. Hicks, R. Thomas, A. Potter, M. Collins, M. Linders, C. Fimbel, S. Black, H. E. Anderson, G. Diehl, S. Hamman, R. Gilbert, J. Foster, D. Hays, D. Wilderman, R. Davenport, E. Steel, N. Page, P. L. Lilley, J. Heron, N. Kroecker, C. Webb, and B. Reader. 2011. Conservation of prairie-oak butterflies in Oregon, Washington, and British Columbia. *Northwest Science* 85:361-388.
- Shaben, J., and J. H. Myers. 2010. Relationships between Scotch broom (*Cytisus scoparius*), soil nutrients, and plant diversity in the Garry oak savannah ecosystem. *Plant Ecology* 207:81-91.
- Stevens, C. J., N. B. Dise, J. O. Mountford, D. J. Gowling. 2004. Impact of nitrogen deposition on the species richness of grasslands. *Science* 303:1876-1879.
- Stock, W. D., K. T. Wienand, and A. C. Baker. 1995. Impacts of invading N₂-fixing *Acacia* species on patterns of nutrient cycling in two Cape ecosystems: evidence from soil incubation studies and ¹⁵N natural abundance values. *Oecologia* 101:375-382.

- Suding, K. N., J. R. Larson, E. Thorsos, H. Steltzer, and W. D. Bowman. 2004. Species effects on resource supply rates: do they influence competitive interactions? *Plant Ecology* 175:47-58.
- Szili-Kovács, T., K. Török, E. L. Tilston, and D. W. Hopkins. 2007. Promoting microbial immobilization of soil nitrogen during restoration of abandoned agricultural fields by organic additions. *Biology and Fertility of Soils* 43:823-828.
- Tilman, D., and D. Wedin. 1991. Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology* 72:685-700.
- Török, K., T. Szili-Kovács, M. Halassy, T. Tóth, Zs. Hayek, M. W. Paschke, and L. J. Wardell. 2000. Immobilization of soil nitrogen as a possible method for the restoration of sandy grassland. *Applied Vegetation Science* 3:7-14.
- Ugolini, F. C., and K. Schlichte. 1973. The effect of Holocene environmental changes on selected western Washington soils. *Soil Science* 116:218-227.
- Vinton, M. A., and E. M. Goergen. 2006. Plant-soil feedbacks contribute to the persistence of *Bromus inermis* in tallgrass prairie. *Ecosystems* 9:967-976.
- Vitousek, P. M., and R. W. Howarth. 1991. Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry* 13:87-115.
- Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and G. D. Tilman. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* 7:737-750.
- Wedin, D. A., and D. Tilman. 1990. Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia* 84:433-441.
- Wedin, D., and D. Tilman. 1993. Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. *Ecological Monographs* 63:199-229.
- Wilson, S. D., and A. K. Gerry. 1995. Strategies for mixed-grass prairie restoration: herbicide, tilling, and nitrogen manipulation. *Restoration Ecology* 3:290-298.
- Witkowski, E. T. F. 1991. Effects of invasive alien *Acacias* on nutrient cycling in the coastal lowlands of the Cape Fynbos. *Journal of Applied Ecology* 28:1-15.
- Zavaleta, E. S., M. R. Shaw, N. R. Chiariello, H. A. Mooney, and C. B. Field. 2003. Additive effects of simulated climate changes, elevated CO₂, and nitrogen deposition on grassland diversity. *Proceedings of the National Academy of Sciences* 100:7650-7654.

Received 31 August 2010

Accepted for publication 5 May 2011